SOME ASPECTS OF THE NITROGEN CYCLE IN A CALIFORNIAN STRAND ECOSYSTEM[1]

BOOKER HOLTON, JR., MICHAEL G. BARBOUR,
and SCOTT N. MARTENS
Department of Botany, University of California,
Davis, CA 95616-8537

ABSTRACT

Nitrogen inputs and storage pools were quantified for 20 months on a perennial grass dominated beach-foredune area at Pt. Reyes National Seashore, CA. Atmospheric input of ammonium and nitrate by bulk precipitation (rain + dry fallout) was 1.6 kg N ha^{-1} yr^{-1} and by summer fog condensation was 4.2 kg N ha^{-1} yr^{-1}. Non-symbiotic nitrogen fixation was not detected and fixation by a nodulated legume species is negligible relative to atmospheric inputs. The total ecosystem nitrogen pool was only 390 kg ha^{-1}, 78% of which was soil organic nitrogen, 18% was in vegetation, and 4% was inorganic soil nitrogen. Living vascular plant tissue contained 1.7% nitrogen—a value typical of crop plants on fertile soil—despite soil nitrogen content <0.006%.

Dune sands are often deficient in many plant nutrients, particularly nitrogen. Nitrogen levels of 0.006–0.02% have been measured in dune sands dominated by the dune grass *Ammophila arenaria* (Willis et al. 1959; Hassouna and Wareing 1964; Barbour 1970), whereas typical soil nitrogen values for cultivated soils fall within the 0.06–0.5% range (Bremner 1965). Low soil nitrogen is intensified in dune sands by low organic matter accumulation and excessive leaching, but the losses may be offset by nitrogen inputs from sources unique to the beach-dune environment, such as wave-deposited organic debris, nitrogen fixation, sea spray, and fog (Wilson 1959; Wagner 1964; Berenyi 1966; Ranwell 1972; van der Valk 1974a, b). In general, quantitative data for such inputs along the California coast have not been published.

An objective of this study was to quantify some of the storage pools and transfer processes thought to be important in a conceptual, first approximation model of a nitrogen cycle in a northern California strand. The storage pools to be identified and quantified were: 1) nitrogen bound in the vegetation, 2) nitrogen bound in the organic soil fraction, and 3) nitrogen in the inorganic soil fraction. Nitrogen inputs to be identified and quantified were: 1) precipitation, 2) fog and sea spray, and 3) biological nitrogen fixation.

[1] Correspondence should be sent to Michael G. Barbour.

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Study Area

A study site on the ocean-facing beach at Point Reyes National Seashore (38°N and 123°W) was selected with the cooperation of the National Park Service. The study extended from April 1975 through January 1977. The beach extends in a N–S direction 18 km between Point Reyes in the south and the Tomales Point headland at Kehoe Creek. The biota and physical environment of the area have been described by Elliott and Wehausen (1974), Grams et al. (1977), Holton and Johnson (1979), Barbour (1978), Holton (1980), and Barbour et al. (1982). Along this beach, stabilized dunes form narrow ridges parallel to the prevailing wind direction, extending 0.5–2.0 km inland onto coastal grassland. These dunes are perched on cliffs composed chiefly of Monterey Shale and are therefore cut off from invasion by beach sands except at points where the cliff is low or absent. Inland sand movement has, within the past 50 yr, been additionally slowed by a foredune formed by the sand-stilling qualities of the introduced European beachgrass, *Ammophila arenaria*.

The climate at Point Reyes falls under the Koppen class of Csb (Durrenberger 1974): a temperate, mediterranean climate with mild, rainy winters and cool, dry summers. During the summer months, the Pacific Subtropical High lies over the ocean to the west, and air descending from this high produces moderate northwest to west winds which cross the coast. Oceanic upwelling cools the air offshore, causing frequent fog during the night and early morning hours. During the fall, the westerlies shift southward and frontal passages produce showers and rain. Generally, about 90% of the 610 mm annual precipitation falls from November through April. Mean annual temperature is 11.4°C, and the range between the means of the hottest and coldest months is moderated by proximity to the ocean to only 3.7°C (U.S. Weather Bureau, Climatological Data, California Section, 1913–1974; Howell 1970).

A representative 0.5 km long portion of the beach was subjectively chosen for field work. The beach consisted of a lower portion devoid of vegetation, an upper portion which exhibited scattered cover by about seven species, and a foredune more densely covered by perennial grasses.

The lower beach extended approximately 40 m from mean tide line inland to the leading edge of vegetation. Elevation rise was approximately 2 m. This region included a berm and rows of detritus deposited at the most recent highest tide marks. The upper beach exhibited 10% cover by scattered clumps of *Atriplex leucophylla, Abronia latifolia, Ammophila arenaria, Cakile maritima, Leymus mollis* (Trin) Pilger, *Ambrosia chamissonis, Lathyrus littoralis,* and several less common species. This portion of the beach was approximately 25 m wide and included an additional 2 m increase in elevation above mean tidal datum. The foredune was densely covered with *Ammophila arenaria* and *Leymus mollis,* reaching 100% cover but averaging 60% cover. Foredune height averaged 3 m above the upper beach. Plant nomenclature follows Munz (1968) except for *Leymus mollis.*

Methods

Nitrogen input in bulk precipitation and fog condensation. Bulk precipitation was collected biweekly from June 1975 through March 1976, in three devices similar to those described by Carlisle et al. (1966) and as modified by Reiners (1972). The collectors were placed at equal intervals along the 0.5 km of beach front, positioned at the top of the foredune but away from vegetation. These collectors consisted of 4 liter Nalgene bottles, fitted with Nalgene funnels (17 cm outside diameter). The funnels were plugged with nylon wool and covered with nylon mesh to keep out wind-blown debris. The bottles were painted with aluminum paint to retard algal growth, and a few crystals of phenol were placed into each bottle prior to each sampling period to inhibit bacterial growth. These bottles were buried to within 30 cm of the top of the funnels. Rainfall was measured with a portable rain gauge placed near the bottles.

Fog condensation was collected biweekly during the summer of 1975, using three collection screens similar to those of Azevedo and Morgan (1974). An aluminum screen (18 × 16 mm mesh) rolled into a tube, 76 cm long and 8 cm in diameter, was placed on top of each of the three funnel-bottle assemblies described earlier. This fog collection assembly extended about 1 m above ground. Summer fog along the coast condenses on plants during the cool morning hours, and dune grasses reach up to 1 m above the ground surface; therefore, collection screens 1 m high simulated this vegetation.

The three fog traps were placed near the bulk precipitation collectors on or near the top of the foredune, away from obstructing vegetation. Precautions against algal and bacterial growth were as earlier described.

All bulk precipitation and condensed fog samples were refrigerated (4°C) for later chemical analyses. Nitrate in all water samples was determined by the phenoldisulfonic acid method (Chapman and Pratt 1961). The water samples were pretreated with silver sulfate to remove interfering chloride ions. Ammonium in the water was determined with an Orion specific ion electrode. Salinity level was estimated from conductivity measurements using a Lectro Mhometer (Lab-Line, Inc.).

Nitrogen in soil. Soils were sampled at eight locations along the

0.5 km of beach front. Root-free samples were taken at the surface and at depths of 20 cm and 40 cm. At each of the eight locations, samples were taken at four topographic positions: tide-mark, seaward foredune face, foredune top, and landward foredune face. All samples were kept in sealed plastic bags, stored at 4°C, and chemically analyzed within 2 wk. Nitrate and ammonium were determined as for water samples and organic nitrogen was determined by macro-Kjeldahl analysis. Soils were sampled in June 1975 and September 1976.

Nitrogen in plant tissue. Standing above-ground biomass was sampled in September 1976 from a series of clippings within quadrats of varying sizes. Since the two grasses *Leymus mollis* and *Ammophila arenaria* dominate the dune plant cover, sampling was limited to only these species.

Optimum sampling area for each species was determined using the nested quadrat method of Wiegert (1962). This method enables an optimal choice of quadrat size to be made, based on cost in time and labor and on sampling precision. On the basis of minimal cost and reduced within-plot sample variance, a quadrat size of 0.15 m^2 was selected for *Ammophila* stands and one of 1.0 m^2 for *Leymus*-dominated stands. (*Leymus* stands are much less dense than *Ammophila* stands, 30–60% cover, as opposed to 80–100% cover.)

In the field, a grid of contiguous plots was laid out within subjectively chosen foredune stands of each grass type. The stands were selected as representative of foredune vegetation within the 0.5 km length of beach. The size of the *Ammophila* grid was 6 × 3 m and that for the *Leymus* grid was 6 × 6 m. Each grid was replicated three times. The size of the cells composing each grid was the same as the respective quadrat sizes mentioned above.

Within each grid, 12 randomly selected quadrats were clipped to ground level. Clippings were separated into living and dead components, oven-dried at 70°C for 72 hr, and weighed. Samples used for chemical analysis were milled in a Wiley mill to 40-mesh and stored at room temperature in screw-capped jars. Nitrogen was determined by macro-Kjeldahl analysis.

Other plant species of lesser cover were not sampled for biomass estimation, but above-ground tissue was collected in the upper beach at several times through the late summer and winter of 1976 and analyzed for nitrogen.

Below-ground biomass was estimated from 12 quadrats subjectively placed on representative foredune vegetation along the 0.5 km of beach. Six 1.0 m^2 quadrats were placed in *Leymus*-dominated stands, and six 0.15 m^2 quadrats were placed in *Ammophila*-dominated stands. Cover was 30–100%, as for above-ground samples. Sand was excavated beneath each quadrat to a depth of 40 cm and later sieved to separate root material from sand. Roots were oven-dried at 70°C for 72 hr and weighed. No nitrogen analyses of root tissue were made.

Estimates of nitrogen-fixation in the soil. Selected dune plants were assayed for the ability to fix nitrogen by the acetylene reduction technique (Stewart et al. 1967; Hardy et al. 1968; Waugham 1971, 1972). This method measures the reduction of acetylene to ethylene by the nitrogenase enzyme system common to all nitrogen-fixing organisms.

Rhizosphere soil, roots, and (where present) nodules were collected randomly along the 0.5 km length of upper beach at various soil depths and at several times between August 1976 and January 1977. Soil and roots of the dominant grasses and excised nodules of legumes were incubated in a 10% acetylene–air mixture in rubber-stoppered 25 ml serum tubes. The same material incubated in air alone served as controls.

Gas samples were subsequently withdrawn and subjected to analysis with a gas chromatograph (Perkin-Elmer model 3920B) equipped with a hydrogen flame ionization detector. Acetylene and ethylene were separated on a column (0.3 × 122 cm) filled with Poropak-R (100–200 mesh). Nitrogen gas served as a carrier at a flow rate of 30 ml min^{-1} and a temperature of 45°C.

Results and Discussion

Nitrogen in bulk precipitation and fog condensation. The seasonal precipitation total of 254 mm (Fig. 1) was considerably below the normal yearly average of 610 mm, because 1975–1976 was the first of a 2-yr drought period. Rainfall measurements made with portable rain gauges correlated well with volume of precipitation in the collection bottles ($r = 0.99$).

Ammonium-N and nitrate-N concentrations in bulk precipitation varied with collection period (Fig. 2). The concentration of ammonium-N ranged from trace amounts to about 7 ppm, averaging 1.10 ppm. Nitrate-N concentrations were extremely low, ranging from trace amounts to 1.0 ppm, with an average concentration of 0.15 ppm.

Ammonium-N concentration was positively correlated with the salinity of the precipitation, a relationship which may indicate an oceanic source of this form of nitrogen. Such a relationship did not exist for nitrate. The concentration of both salt and ammonium-N decreased with increased rainfall above a threshold value of 0.2 liter of collected rainwater, which is equivalent to 7 mm of precipitation. Thus, during periods of little or no precipitation, dry fallout of dust and particulate material from sea spray would be relatively more concentrated in salts and ammonium.

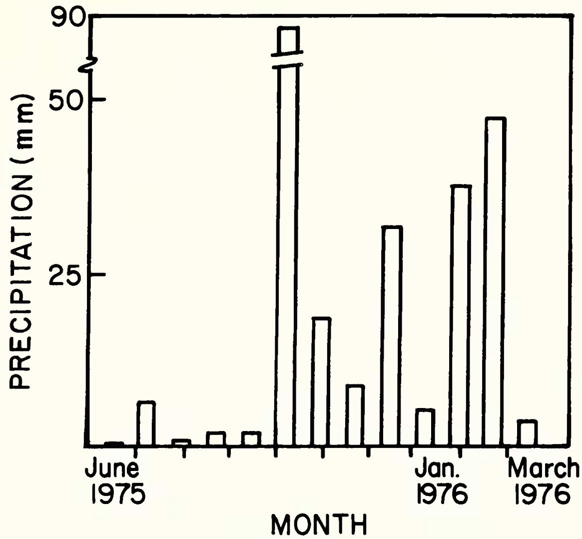

FIG. 1. Bulk precipitation, collected biweekly, June 1975–March 1976 at Pt. Reyes National Seashore, CA.

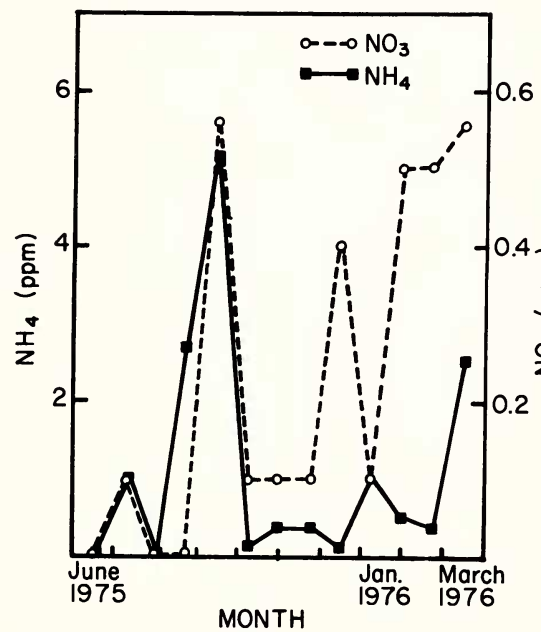

FIG. 2. Nitrate-N and ammonium-N content of bulk precipitation samples collected between June 1975 and March 1976 at Pt. Reyes National Seashore, CA.

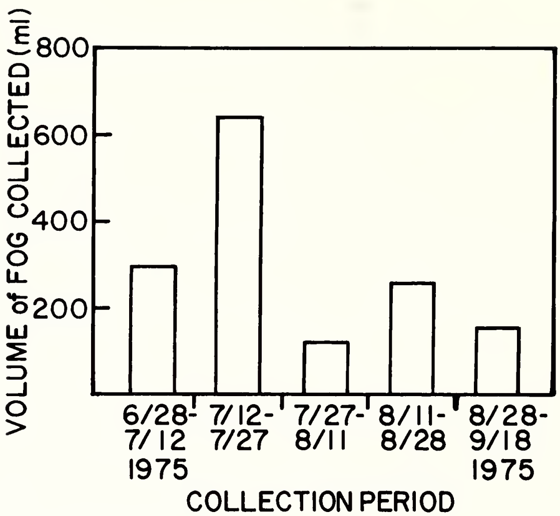

FIG. 3. Fog condensation collected biweekly, June–September 1975 at Pt. Reyes National Seashore, CA.

The annual nitrogen input in bulk precipitation can be calculated from data on precipitation volume per unit collection surface area, and from the concentrations of both ammonium-N and nitrate-N per collection period, summed over the rainfall season. This annual input is estimated to be 1.6 kg ha^{-1}. Of this total, 0.9 kg is ammonium-N, and 0.7 kg is nitrate-N.

The annual nitrate-N (0.7 kg ha^{-1}) and ammonium-N (0.9 kg ha^{-1}) inputs in bulk precipitation measured at Point Reyes compare well with similar measurements at other California sites. At Berkeley, California, about 60 km to the southeast, McColl and Bush (1978) estimated the annual inputs of nitrate-N and ammonium-N; during the precipitation year 1974–1975 they were 1.02 and <0.98 kg ha^{-1}, respectively. For eight northern California sites, McColl et al. (1982) measured an average of 2.5 kg N ha^{-1} in wet and dry ionic fallout during the wet season (November 1978–March 1979). Schlesinger and Hasey (1980) measured 1.0 kg N ha^{-1} yr^{-1} deposition in bulk precipitation at a site 10 km from the coast in the Santa Ynez Mountains of southern California during 1977–1978. A mean of 2.0 kg N ha^{-1} yr^{-1} deposition, mostly in dry fallout, was measured by Schlesinger et al. (1982) in 1978–1980 in the same mountains. Ellis et al. (1983) measured 1.5 kg N ha^{-1} yr^{-1} in bulk precipitation at a site 75 km inland in San Diego County. These N input values are relatively low compared to measurements in eastern regions of the U.S. (Boring et al. 1988), although high N deposition

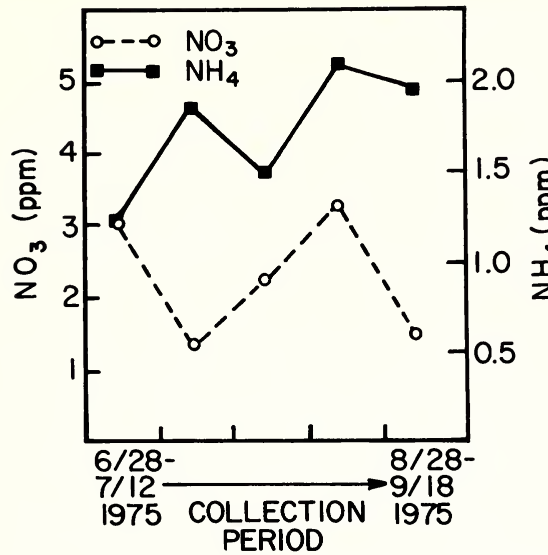

FIG. 4. Nitrate-N and ammonium-N content of fog condensation collected June–September 1975 at Pt. Reyes National Seashore, CA.

(8.2 kg ha^{-1} yr^{-1}) has been reported for the urbanized Los Angeles basin of California (Riggan et al. 1985).

Judging from data collected by Barbour et al. (1973) for nearby Bodega Head, about 60% of all foggy days in a typical year occur in our sampled period between June and September (Fig. 3). Salt concentration of condensed fog decreased with collection volume. The concentration of ammonium-N and nitrate-N varied with collection period (Fig. 4). Ammonium-N ranged from 1.2 to 2.5 ppm, averaging 1.72 ppm. Nitrate-N ranged from 1.0 to 6.0 ppm, with an average of 2.45 ppm. Nitrogen input by summer fog condensation can be calculated from data on screen surface area, condensation volume, and concentrations of ammonium-N and nitrate-N per collection period. This nitrogen contribution was approximately 2.5 kg ha^{-1} during the sampling period, with 1.4 kg from nitrate and 1.1 kg from ammonium sources.

Extrapolation from collection screens to a ground-level surface area or to a vegetation canopy may overestimate total nitrogen input. A rigid, vertical screen extending 1 m above the ground may be a more efficient sea spray or fog collector than a horizontal surface near the ground or a leaf surface in a vegetation canopy. Barbour (1978) found this to be the case for salt spray deposition on the beach at Point Reyes.

Fog condensation is likely to be a significant N source for the

TABLE 1. TOTAL NITROGEN, NITRATE, AND AMMONIUM IN SAND COLLECTED AT SEVERAL DEPTHS IN THE FOREDUNE AT PT. REYES NATIONAL SEASHORE, CA. Values expressed as mean (±SE). n = 24 for total nitrogen, 17 for nitrate and ammonium. Soil collected in summers of 1975 and 1976.

Soil depth (cm)	% nitrogen	ppm NO_3^--N	ppm NH_4^+-N
Surface	0.003 (0.001)	0	0
20	0.004 (0.001)	1.88 (0.37)	1.52 (0.10)
40	0.006 (0.001)	0.65 (0.11)	0.74 (0.18)

coastal strand ecosystem. Azevedo and Morgan (1974) showed the importance of fog drip in two coastal forests of northern California. Fog water collected in these forests averaged 1.7 and 4.1 ppm ammonium-N, which is similar to the 1.7 ppm ammonium-N we measured at Point Reyes. Schlesinger and Hasey (1980) found significant fog drip in collectors mounted with artificial foliage. They attributed the increased nitrogen deposition in these collectors to more efficient interception of dry aerosols. Jacob et al. (1985) measured 0.6–4.6 ppm ammonium-N and 0.08–7.4 ppm nitrate-N in fogwater collected in August 1982 at Pt. Reyes. When an offshore wind prevailed, fogwater had less sea salt and more soil dust and automobile exhaust than when onshore winds prevailed.

Nitrogen in soil. No significant differences could be detected in soil nitrogen between the seaward foredune face, landward face, and the top. Values were very low, 0.003–0.006%, depending on depth (Table 1). In comparison, higher soil nitrogen values were associated with the tide-mark (0.006–0.01%) and the stabilized dune (0.04–0.2%), again depending on depth. The available inorganic nitrogen pool in the foredune was low, <2 ppm of nitrate-N or ammonium-N (Table 1).

Using an average bulk density = 1.51 g cm^{-3}, organic N percentage by weight = 0.005%, average concentrations of nitrate-N = 1.3 ppm, and ammonium-N = 1.2 ppm, we estimated the organically bound soil nitrogen pool to be approximately 302 kg ha^{-1} to a depth of 40 cm, and the available soil nitrogen pool, to the same depth, to be 15 kg ha^{-1}.

TABLE 2. MEAN (±SE) ABOVE-GROUND BIOMASS (G M^{-2}) IN REPRESENTATIVE FOREDUNE PATCHES OF *LEYMUS* AND *AMMOPHILA* AT PT. REYES NATIONAL SEASHORE, CA. Material collected in September, 1976. n = 36.

Species	Living	Dead	Total
Leymus mollis	129.4 (23.7)	82.6 (12.0)	211.9 (33.5)
Ammophila arenaria	445.7 (58.0)	188.4 (23.7)	632.1 (76.3)

TABLE 3. NITROGEN IN ABOVE-GROUND LIVING TISSUE OF UPPER BEACH SPECIES COLLECTED IN FALL AND WINTER, 1976 AT PT. REYES NATIONAL SEASHORE, CA.

Species	n (%)
Abronia latifolia	1.52
Ammophila arenaria	1.40
Atriplex leucophylla	2.00
Cakile maritima	2.74
Leymus mollis	2.80
Ambrosia chamissonis	2.54

Nitrogen in plant tissue. Californian upper beaches and foredunes have a very low standing crop biomass, estimated to be 20–400 g m^{-2}, corresponding to that of desert or arid steppe communities (Barbour and Robichaux 1976). The estimated above-ground biomass from our field clippings of *Leymus mollis* and *Ammophila arenaria* falls near the upper part of this range (Table 2).

The average tissue nitrogen concentration of the most common beach and dune plant species at Point Reyes is 1.5–3.0% (Table 3). Dead matter averaged 0.6% N. Stout (1961) and Epstein (1965) considered a tissue nitrogen concentration of 1.5% to be adequate for most plant growth, and to be typical of N content of mesic crop plants. Thus, these strand species have a relatively high nitrogen content, despite a soil substrate which is very low in nitrogen.

Assuming an average tissue nitrogen concentration of 1.7% in the living material and 0.6% in the dead material, bound nitrogen in the above-ground living biomass of the foredune is estimated to be 49.4 kg ha^{-1}, and that bound in the dead material to be 8.2 kg ha^{-1}.

Belowground, our limited number of quadrat excavations to a depth of 40 cm indicated that 70–190 g m^{-2} of live roots, exclusive of the many fine roots, could be expected. Although we did not measure nitrogen content in our root samples, Pavlik (1983a, b) provides data for these same species from Point Reyes. Root nitrogen concentration of greenhouse-grown plants was 0.6%; therefore, the estimated below-ground N content of roots in the foredune is 4.2–11.4 kg ha^{-1}.

The well-developed rhizome systems of *Ammophila* and *Leymus* also contribute significantly to the below-ground nitrogen pool. We did not measure rhizome mass or N content but pertinent data on greenhouse-grown plants are available from Pavlik (1983b). Rhizome nitrogen concentration was 1.0% and rhizome biomass was 27–30% of root biomass. From these data and our measured root biomass data we estimate the minimum below-ground nitrogen pool in rhizomes to be 2.0–5.4 kg ha^{-1}.

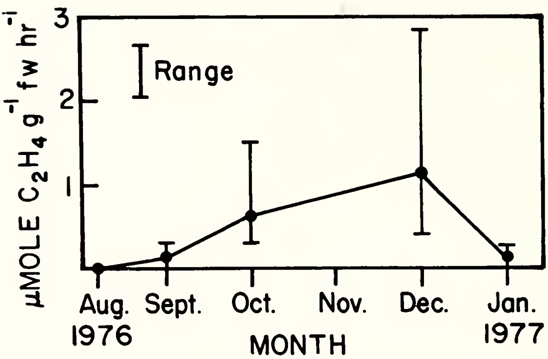

FIG. 5. Seasonal variation in ethylene production from acetylene by nodules of *Lathyrus littoralis* on the upper beach at Pt. Reyes National Seashore, CA.

Nitrogen fixation. Sand cores with associated grass root material, which were routinely assayed using the acetylene reduction technique, failed to show detectable levels of nitrogen fixation under ambient field conditions. Attempts to isolate nitrogen fixing bacteria on artificial N-free media inoculated with dune sand also were negative. These results contrast with those of others (Abdel Wahab 1975; Abdel Wahab and Wareing 1980; Hassouna and Wareing 1964) who have found significant rhizosphere nitrogen fixation in *Ammophila arenaria* in Welsh dunes.

Three leguminous species were found to be nodulated and to have the ability to reduce acetylene to ethylene. Two of these species, *Lupinus arboreus* and *L. chamissonis,* are dominants on the more stabilized, perched dunes, and showed rates of 0.05–0.6 µmol ethylene g^{-1} fresh weight hr^{-1}. Nodules of both species were deep (1–1.5 m) and ranged from 0.1 g to 0.55 g fresh weight.

Lathyrus littoralis is found on the upper beach in a few restricted localities and it is not a dominant. *Lathyrus* had the highest nitrogenase activity of the three, a range of 0.01–2.83 µmol ethylene g^{-1} fresh weight hr^{-1} (Fig. 5). The lower late summer rates were associated with dark-colored, fibrous nodules; higher winter rates were associated with light-colored, fleshy nodules. Most *Lathyrus* nodules were at 30–70 cm depth, and nodule size was 6–60 mg fresh weight.

As we did not estimate nodule biomass per unit of surface area, an extrapolation of our nitrogen-fixation rates to an areal basis is not possible. Considering the low cover by *Lathyrus,* however, the contribution of nitrogen fixation is negligible relative to the atmospheric inputs of nitrogen measured for the strand ecosystem.

Synthesis. Despite the obvious need for additional information to describe the complete nitrogen cycle, a summary of the major pools

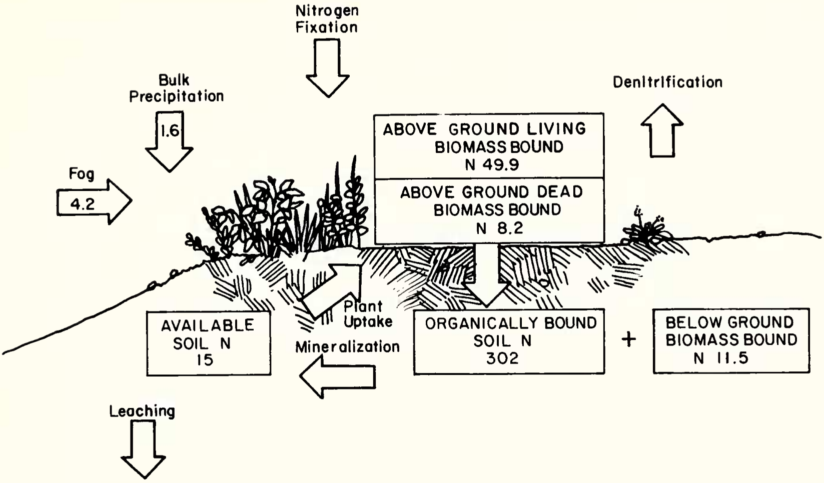

FIG. 6. Annual nitrogen inputs (kg ha^{-1} yr^{-1}) and pools (kg ha^{-1}) examined in this paper.

examined in this paper appears in Figure 6. The total ecosystem nitrogen pool of ~390 kg ha^{-1} is quite low; approximately 78% is soil organic nitrogen, about 4% exists as available soil inorganic nitrogen, and 18% is bound in the biomass.

Nitrogen input in bulk precipitation was 1.6 kg N ha^{-1} yr^{-1} and is similar to other bulk precipitation measurements made in California (McColl and Bush 1978; Schlesinger and Hasey 1980; Schlesinger et al. 1982; Ellis et al. 1983). However, bulk precipitation measurements may underestimate total atmospheric nitrogen deposition by 30–40% because they do not include all forms of wet and dry deposition (Boring et al. 1988).

Fog condensation provided a larger nitrogen input, 4.2 kg N ha^{-1} yr^{-1}, than bulk precipitation. It is difficult to assess the accuracy of this value because we don't know how comparable fog condensation on screens is, to that on natural vegetation. Certainly the same physical processes operate in both cases and fog or cloud condensation has been shown to be an important source of nutrients in other systems (Schlesinger and Hasey 1980; Lovett et al. 1982).

Our preliminary survey of nitrogen fixation, determined by acetylene reduction, did not detect microbial and algal fixation of nitrogen in the free-living or associative forms within the Point Reyes dunes. The nodulated legumes *Lupinus arboreus, L. chamissonis,* and *Lathyrus littoralis* are only locally important on stabilized dunes and on the upper beach and so account for little nitrogen input. In other dune sand systems non-symbiotic (Hassouna and Wareing

1964; Abdel Wahab and Wareing 1980) and symbiotic nitrogen fixation (Gadgil 1971; Sprent 1973) have been shown to provide important nitrogen inputs.

Other possible sources of nitrogen for the coastal strand system include seaweed wrack and seafoam. Wave-deposited and wind-transported seaweed could be an important nitrogen source at the tidemark and upper beach. Holton (1980) showed that the seaweeds *Egregia* and *Macrocystis* decomposed more rapidly and released more nitrogen than the marine angiosperm *Phyllospadix.* Seafoam, a largely algal product with a nitrogen concentration close to that of seaweed, is wind transported and intercepted by vegetation on the foredune and could also be a nitrogen source for the strand ecosystem (S. Wing, personal communication).

The available soil nitrogen pool is small despite measured annual atmospheric inputs which are nearly 40% of its size. The largest output from this pool is probably from leaching. Inorganic nitrogen is easily leached from the coarse sands due to their lack of clay or organic matter for cation retention. Nitrogen loss by denitrification is likely to be low in well-drained sands with low nitrate and organic matter concentrations (Focht and Verstraete 1977).

Development of an extensive root architecture may be one means whereby dune plants are able to maintain adequate tissue nitrogen (1.4–2.8%) despite the low nitrogen status of these dunes. The root length densities under *Ammophila* and *Leymus* at Point Reyes have been reported to be 15–40 m root length per liter of soil (Holton 1980). These densities compare with those reported for more dense stands of grasses (66–548 m liter^{-1}) and sugar-cane (18 m liter^{-1}) reported by Dittmer (1938) and Evans (1938).

Acknowledgments

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